

## Phylogenetic systematics and zoogeography of Australian nudibranchs

### 1. Presence of the aeolid *Godiva quadricolor* (Barnard) in Western Australia

by R.C. Willan

Department of Zoology  
University of Queensland  
St Lucia, Queensland 4067

#### ABSTRACT

The aeolid *Godiva quadricolor* (Barnard, 1927) is newly recorded from Australia on the basis of a population in southwestern Australia. It was first observed about 1980 and it is apparently presently restricted to the Fremantle-Cockburn Sound area. Shipping offers the most plausible explanation for transportation of the original stock from southern Africa. A complete anatomical description is provided to enable its future recognition. The genus *Godiva* Macnae, 1954, which is redefined and its scope restricted to embrace two (probably three) species, is relatively advanced within both the superfamily Aeolidioidea and family Facelinidae. At present the penial spine is the only character that can be identified as an autapomorphy, but it is suggested that, in fact, a suite of apomorphies relating to the penial spine and jaw ornamentation do exist. Eight other aeolids that have been included in *Godiva* at one time or another are discussed and excluded. Although apparently derived from the Facelinidae Vayssière, 1888, the Glaucidae Férussac, 1822 deserves separate familial ranking because of numerous apomorphies acquired during the evolution of its novel pleustonic life style. Phidianidae Odhner in Franc in Grassé, 1968 is confirmed as a junior synonym of Facelinidae.

#### INTRODUCTION

Whilst investigating the intertidal biota encrusting the beacon pylons at the entrance to Cockburn Sound, immediately south of the port of Fremantle, southern Western Australia, on 10 January 1984, Mr Clayton Bryce discovered a medium-sized aeolid nudibranch that he had never seen before (Fig. 1). The specimen was found between middle and low tide levels crawling over mussels

(*Mytilus edulis* L.). It was photographed and taken back to the Western Australian Museum. Unfortunately the animal died before any notes could be made of its appearance in life or habits. Mr Bryce showed me his transparencies in September 1985, and the animal was immediately recognized as new to Australia. Subsequently an anatomical investigation showed it to be *Godiva quadricolor* (Barnard, 1927), an identification that was confirmed beyond all doubt by seeing two slides of South African animals, one of which is reproduced here (Fig. 2). While preparing this report, I received word from Mr Gerhard Saueracker that he had sighted at least a dozen individuals of this species in the Fremantle-Cockburn Sound area between 1980 and 1983. This report describes Mr Bryce's specimen in some detail to enable immediate recognition whenever and wherever further specimens are found.

Besides being a new record for Australia, this particular species is of importance in two other areas of research. The position and scope of the genus *Godiva*, of which *G. quadricolor* is the type species, needs appraisal in a phylogenetic context and the occurrence of *G. quadricolor* in temperate Western Australian waters is vexing zoogeographically. Both these aspects (i.e., phylogenetic systematics and zoogeography), which are addressed in this paper, are currently receiving vigorous attention in zoological circles. This paper is the first of an intended series that I will publish in this Journal discussing phylogenetic systematics and zoogeography of Australian nudibranchs.

## FAMILY FACELINIDAE VAYSSIÈRE, 1888 *Godiva quadricolor* (Barnard, 1927) (Figs 1-13)

### SYNONYMY

*Hervia quadricolor* Barnard, 1927, p. 203, pl. 20, figs 9, 10.

*Godiva quadricolor* (Barnard): Macnae, 1954, pp. 23-25, text figs 14-16; Edmunds, 1964, pp. 26, 27; Lemche, 1964, pp. 56, 57; Baba & Hamatani, 1965, pp. 108, 109; Edmunds, 1977, pp. 302, 303; Rudman, 1980, pp. 160, 171; J. Garcia & F. Garcia, 1984, p. 14.

*Godiva* Macnae has been placed on the Official List of Generic Names in Zoology with the name number 1717 (I.C.Z.N., 1966, Opinion 778). The name *quadricolor* Barnard, as published in the binomen *Hervia quadricolor* (type species of *Godiva* Macnae), has been placed on the Official List of Specific Names in Zoology with name number 2148 (I.C.Z.N., 1966, Opinion 778).

### DESCRIPTION OF AUSTRALIAN SPECIMEN

When crawling in the fully extended state (Fig. 1), the animal (WAM 339-86) was approximately 30 mm long. Its body, which was elongate and widest at the level of the first ceratal cluster, was evenly rounded (circular in cross section) and relatively high. The foot was broader than the back and it tapered posteriorly to a long, narrow tail; anteriorly the foot was extended into two, relatively short tentaculiform processes. The anterior margin of the head was bilobed. The prominent oral tentacles were very elongate (twice the length of the rhinophores), narrow, circular in cross section, and they tapered evenly and gradually to sharply pointed extremities. The rhinophores were tall, circular throughout their length, and they tapered to pointed extremities. The rhinophores appeared smooth to the naked eye and under low magnification, but higher magnification (> 10 times) revealed numerous, tiny, low, flat pustules over the entire surface. One photograph of the living animal gave the impression that its rhinophores possessed about five, indistinct, well separated annulations on their proximal third, but annulations could not be detected on the rhinophores when the animal was preserved so I assume it had contracted its rhinophores immediately before being photographed.

From the photographs, it is obvious that the cerata were assembled in distinct clusters with the widest gap between the first (i.e., pre-pericardial) and second (i.e., post-pericardial) clusters. The ceratal clusters were arranged in symmetrical arches on either side of the midline apart from the posterior pairs which were in short oblique rows. All the anterior clusters possessed multiple rows



Figure 1: *Godiva quadricolor*, crawling length approx. 30 mm; found on mussels between mid- and low tide levels, beacon pylon at entrance to Cockburn Sound, southern Western Australia, 10 January 1984. Photo: C. Bryce.



Figure 2. *Godiva quadricolor*, crawling length approx. 20 mm; collected intertidally at Hottentot's Huisie, Oudekraal, Atlantic coast of Cape Peninsula, Cape Town, South Africa, May 1981. Photo: T.M. Gosliner.

of cerata, but the actual number of cerata within a cluster was impossible to determine as most of the cerata had been autotomized when the animal died. Each cerata was elongate and fusiform, and the largest cerata were situated closest to the dorsal midline. The genital apertures were located on the right side at the base of the anterior limb of the first ceratal cluster. The renal pore was situated immediately in front of the base of the anterior limb of the second ceratal cluster (i.e., it is interhepatic). The anus opened high inside the arch of the second ceratal cluster on the right side (i.e., in the cleioproctic position).

The body wall was translucent, the upper half being suffused with pale fawn and darkening mid-dorsally. Numerous, small, irregular, bluish-white speckles overlaid this ground colour particularly dorsally where, over the pericardium and back, they coalesced into blotches. A narrow, cream streak with a mid-central, brown hair line extended mid-dorsally the full length of the tail. The foot and its tentaculiform processes were translucent white. The head in front of the rhinophores was suffused with orange-brown pigment; that behind the rhinophores was pale, translucent cream. The oral tentacles displayed the most distinctive element of the colour pattern. Their distal third was pale creamish-white dorsally in contrast to the remaining (i.e., proximal) two-thirds over which the brownish orange (most intense dorsally) colour was interrupted dorso-laterally by a sharply defined, pale, watery sky blue streak that extended to the base of each rhinophore, gradually widening as it did so. The rhinophores were translucent; their distal third being uniform, pale, creamish yellow in weak contrast to the proximal two-thirds which was brown. There was a faint brown ring at the very base. All the cerata were similarly coloured; the translucency of their epithelium allowed the narrow, chocolate-brown digestive diverticulum to be discerned with ease. Many cerata possessed a dusting of white pigment over their epithelium. The cnidosac was cream or creamish yellow. Below the cnidosac (i.e., towards the upper fifth of the cerata) was a sky blue ring that was more intensely blue than the colour of the streak on the oral tentacles. Below this blue ring (i.e., towards the upper third of the cerata) was a slightly broader orange ring. The blue ring was not contiguous with either the yellow cnidosac above or the orange ring below.

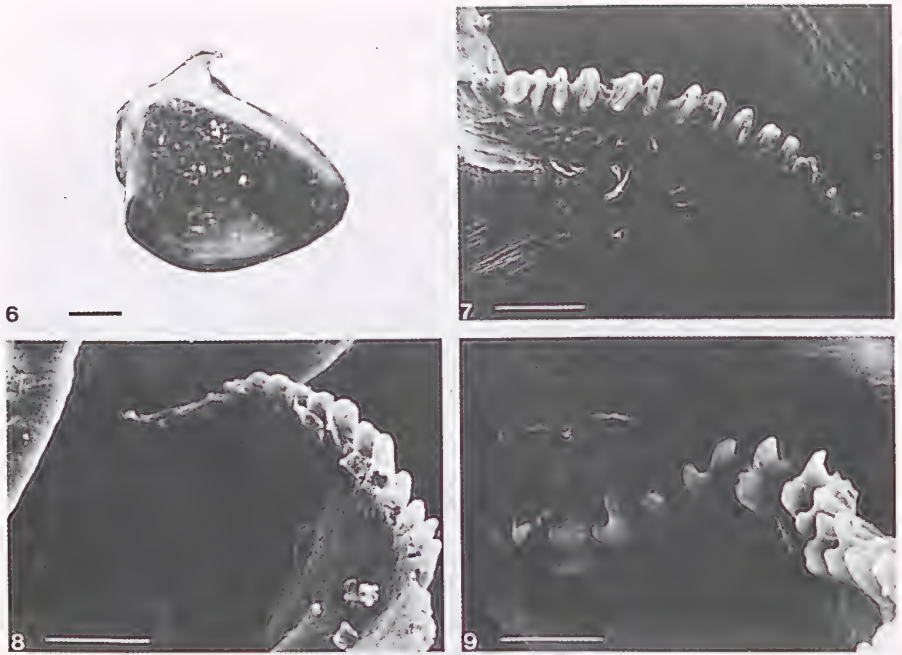
The uniseriate radula contained 30 teeth of which the youngest one was unthickened. All the teeth consisted of a highly arched basal plate with tapered extensions at the postero-lateral corners. The anterior margin was moderately protracted (i.e., extended well beyond the basal plate) and it culminated in a strong, sharp pointed, smooth bladed cusp. Flanking the cusp were five or six (exceptionally seven or eight), strong, narrow, elongate, primary denticles (Figs 3-5) and one tooth also had considerably weaker secondary denticles arising between the primary ones from the blade (Figs 4, 5). The primary denticles decreased progressively in size with the outermost always being smallest. The actual number of primary denticles was found to vary both between and within teeth i.e., there were different numbers of denticles on either side of the blade. Subdenticles were never present on the sides of the primary or secondary denticles.

The jaws (Fig. 6) measured 7.1 mm in vertical height and 8.6 mm in maximum length. Their shape was not quite ovate, being slightly elongate antero-posteriorly. Both jaws were symmetrical and, when viewed in profile, both were strongly convex. In outline, the jaw's sides formed an inequilateral triangle. The posterior side was longest (8.9 mm) with a slightly convex curve. The postero-ventral corner was somewhat produced and relatively acute. The ventral side was straight. The upper two-thirds of the anterior side was heavily cuticularized and it bore a flange that extended, as a thin and transparent shield, beyond the jaw's margin. Immediately adjacent to this flange, the apical section of both jaws bore numerous, irregular, short, cuticularized ridges. The lower third of the anterior side had a shallow notch. The tapering masticatory process was relatively short (i.e., approximately one-third the length of the posterior edge) and thin. Its dorsal margin possessed a single row of tall, cuticularized denticles that were fairly even in size. The denticles closest to the jaw's hinge on the attached region of the masticatory border were absent (presumably worn away through use) but it was possible to count 25 on the free region of the masticatory border. Examination with the SEM revealed that the 13 innermost denticles (i.e., those on the proximal region of the free masticatory border) were peg-like with rounded, unnotched apices (Fig. 7), and the 12 outermost (i.e., the remaining denticles nearer the distal extremity of the free masticatory border) denticles were bilobed (Figs 8, 9) and one was serrated (Fig. 9).

The dialic reproductive system was relatively simple (Fig. 10). The ovotestis, which entirely filled the posterior half of the visceral cavity, was composed of about 30, discrete, dorso-ventrally



Figures 3-5: SEM's showing radular structure of Australian *Godiva quadricolor*. 3, dorsal view of radular teeth (numbers 23 [on left hand side]-27 [on right hand side] towards older end of radula; 4, profile of same teeth (numbers 23-26) to show denticulation; 5, single radular tooth (number 24) enlarged to show secondary denticles between the primary ones. Bars (in Figs 3 and 4) = 0.1 mm and (in Fig. 5) = 0.05 mm.



Figures 6-9: Jaw structure of Australian *Godiva quadricolor*. 6, entire left jaw laid flat showing inner surface, Bar = 2 mm; 7, SEM of simple (i.e., uncleft) denticles on proximal region of free masticatory border; 8, SEM of denticles (simple proximally and bilobed distally) on distal section of free masticatory border; 9, SEM showing detail of bilobed denticles near distal extremity of free masticatory border. Bars (in Figs 7 and 8) = 0.1 mm and (in Fig. 9) = 0.05 mm.

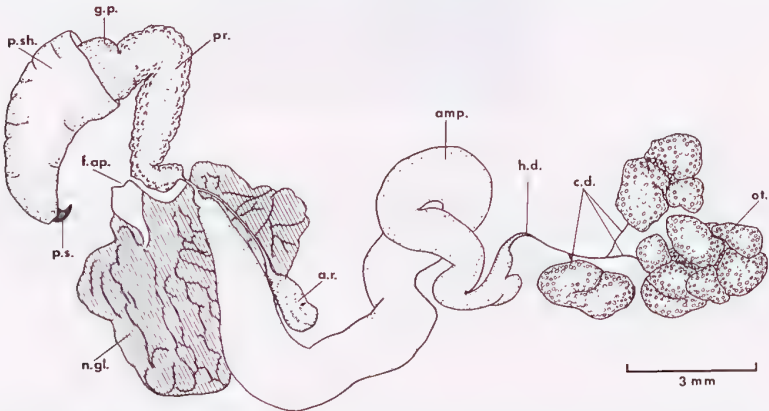
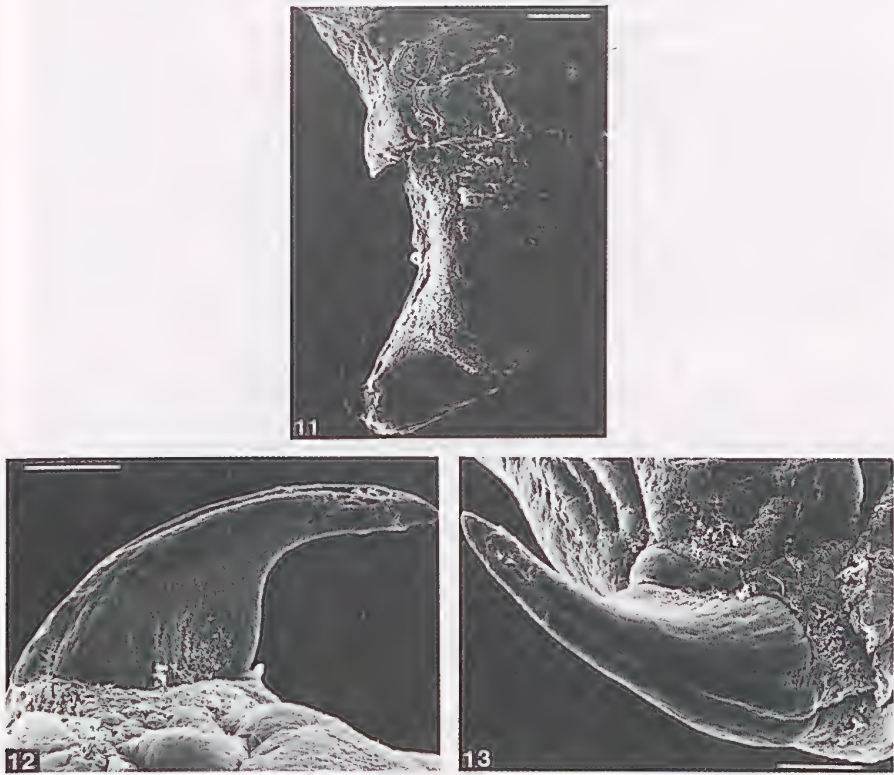


Figure 10: Diagrammatic view of structure of unraveled reproductive organs of Australian *Godiva quadricolor* (penial sheath not removed; only about one quarter of gonadal follicles shown). Abbreviations: amp. = ampullar region of hermaphrodite duct; ar. = allosperm receptacle; c.d. = collecting ducts from ovotestis follicles; f. ap. = female genital aperture; g.p. = glandular proximal region of penis; h.d. = proximal section of hermaphrodite duct; n.gl. = nidamental glands; ot. = ovotestis follicles (detail shown in only one); p.s. = penial spine; p.sh. = penial sheath; pr. = prostatic vas deferens.



Figures 11-13: SEM's of terminal male genitalia of Australian *Godiva quadricolor*. 11, right profile of entire penis with terminal spine (penial sheath not removed), Bar = 0.05 mm; 12, right lateral view showing detail of penial spine; 13, dorsal view showing detail of penial spine and longitudinal groove on outer face. Bars (in Figs 12 and 13) = 0.1 mm.

compressed follicles, each consisting of minute, spherical acini. Approximately 200 acini were present in the anteriormost follicle. The collecting ducts and proximal hermaphrodite duct were exceedingly fine; the latter soon expanded into a long ampulla that continued to enlarge along its length, being the duct of greatest diameter (and hence most easily recognizable) in the entire reproductive system. The ampulla was almost circular in cross section and was completely filled with spermatozoa. The proximal section was arranged into a figure of eight and it was compressed onto the rear of the genital mass. The distal section passed anteriorly without decreasing in diameter. The two halves of the nidamental glands (i.e., the translucent cream mucous gland and milky-white albumen gland) folded so as to sandwich the ampulla laterally. The ampulla eventually constricted to a short distal hermaphrodite duct, gave off a side branch to the single allosperm receptacle, and passed — whilst still very thin — into the vas deferens. The vas deferens was immediately enlarged into a prostate gland and it was glandular for its entire length, being smaller in diameter than the ampulla. The prostate passed into the large, muscular, elongate and slightly curved penis which was surrounded by a muscular sheath (Figs 10, 11). The proximal section of the penis (i.e., that part immediately adjacent to the prostate gland) seemed to possess numerous, distinct, lobular glands but this was not confirmed histologically. A sharp-pointed, curved, cuticular spine (Figs 11-13) measuring 0.4 mm in length projected from the tip of the penis and pointed backwards. The SEM revealed the presence of a narrow, relatively shallow groove along the outer, convex face of the penial spine (Fig. 13). This groove, which was continuous with the terminal opening of the penis, did not extend to the very tip of the spine but ended in a cavity one-tenth of the distance before the end of the spine. The duct to the allosperm receptacle was very long, three times the length of the receptacle, and narrow. The receptacle itself pointed rearwards and was surrounded by the nidamental glands laterally and convolutions of the ampulla posteriorly. In this particular animal, the allosperm receptacle was not expanded, indicating the specimen was virgin. In mated animals the receptacle is much larger, longer, and sausage-shaped.

### ADDITIONAL MATERIAL

Mr Saueracker has provided his additional sightings of *Godiva quadricolor* in southwestern Australia. Apparently none of these specimens was collected:

- 1 specimen (approx. 40 mm crawling length), Outer Estuary, Swan River, southwestern Australia, 1979 or 1980.
- 2 specimens (approx. length of larger specimen 50 mm), North Mole area, Fremantle, southwestern Australia, 1982.
- Approx. 10 specimens, 1-6 metres, Palm Beach, Rockingham, Cockburn Sound, southwestern Australia, 1983.

### REMARKS

The striking external features of *Godiva quadricolor* (Figs 1 and 2) are its translucent body and foot, long tail, long oral tentacles, smooth rhinophores, pale blue streak extending from the rhinophores dorso-laterally down each oral tentacle and elongate cerata with conspicuous blue and orange rings below the yellow cnidosac. Its behaviour is also characteristic — highly active, pugnacious, readily "bristling" the cerata when disturbed and autotomizing the cerata with little provocation.

The body shape, proportions and arrangement of external appendages, colour, shape of radular teeth, and details of jaws of this Australian specimen of *Godiva quadricolor* perfectly match those of southern African animals. (Barnard's (1927) type locality is False Bay, near Cape of Good Hope, South Africa.) The reproductive system, and especially the terminal male genitalia, are also identical. The only differences were the greater number (five or six, exceptionally seven or eight) of primary denticles on all radular teeth and presence of secondary denticles on one tooth in this Australian specimen (Figs 3-5) as compared with only three or four primaries and no secondary denticles in the southern African material.

There is a more recent and more thorough description of South African *Godiva quadricolor* by Macnae (1954). It was based on large numbers of living specimens, so intraspecific variability



was taken into account, and this is apparently considerable as regards colour. Macnae (1954, p. 23) explained how the colours on the cerata varied in their extent; indeed he stated that (presumably any) "one or more of them may be reduced to a vestige or absent altogether". Fortunately the problem of intraspecific colour variation cannot confuse the identification of *G. quadricolor* because all the Australian specimens exactly matched Barnard's (1927) original material in coloration.

Within Australian waters, there are no other known aeolids that could easily be confused with *Godiva quadricolor*, even in the field. Its size, shape, coloration, behaviour and essentially littoral occurrence are reminiscent of the *Austraeolis* species (i.e., *A. ornata* (Angas) and *A. westralis* Burn), but they have shorter oral tentacles, shorter annulate rhinophores, numerous distinct blue spots on the body and foot, and they lack coloured streaks on the oral tentacles and rings on the cerata. In coloration of the cerata only, *Spurilla australis* Rudman is superficially close to *G. quadricolor*; however, despite having two similarly coloured rings on its cerata, *S. australis* has them in reverse order i.e., the orange one is closer to the cnidosac. The only other species of *Godiva* reported from Australia, *G. rachelae* Rudman, is completely different in coloration — it has a pair of orange lines on each side of the head, the lower two-thirds of the cerata is reddish orange, the distal section of the digestive gland is purple and there is a single creamish yellow ring just below the apex of each ceras.

Gosliner (1980) recorded *Godiva quadricolor* from Hawaii and identified Zahl's (1959, p. 523) colour photograph as belonging to that species. However, Dr Gosliner has subsequently studied living specimens of true *G. quadricolor* from South Africa (see Fig. 2) and he now believes the Hawaiian animals represent a distinct species (pers. comm., 1986). Certain disagreements in coloration and reproductive system are also apparent to me between the descriptions of South African and Western Australian material on one hand, and Hawaiian material on the other. Judging from Zahl's photograph and Gosliner's description, Hawaiian animals differ in possessing a white streak along the front edge of the foot and tentaculiform processes and a more or less continuous pale blue line bordering the foot. The tail has a white mid-dorsal streak on its upper surface. The rhinophores are banded in orange-brown and cream. The body is translucent with nebulous pale blue patches. The sky blue dorso-lateral streak is absent from the oral tentacles. The translucent cerata have scattered pigmentation consisting of creamish white pigment, as diffuse yet broad rings, over their outer surface. The chocolate brown digestive diverticulum is straight and narrow, and it tapers gradually to an exceedingly fine distal extremity. The radula of Hawaiian animals appears to be identical to that of South African ones. Gosliner (1980) indicated a spherical allosperm receptacle in Hawaiian animals and he also mentioned a somewhat different orientation for that organ with respect to others of the reproductive system. Closer investigations may reveal even more differences and confirm that the Hawaiian animals represent a new species.

## PHYLOGENETICS

*Hervia quadricolor* Barnard is the type species, by original designation, of the genus *Godiva* Macnae. When Macnae established *Godiva*, he nominated its two principal diagnostic characters (i.e., the most important features by which it could be differentiated from other favorine aeolid genera) as "cerata are inserted in two or more series" [within each cluster] and "rhinophores are either simple or wrinkled". Additional characters shared by *G. quadricolor* and other favorine genera were tentaculiform antero-lateral foot corners, protracted cusp to, and strong primary denticles on, radular teeth and penis "armed with a single terminal hook or unarmed." The fact that the three most important characters of the six (i.e., ceratal arrangement, rhinophoral ornamentation and penial armature) encompassed more than one state meant that interpretation of the generic limits was bound to be controversial and ambiguous, as indeed it has been. What is required now is a critical reappraisal of all the characters of *Godiva quadricolor* to separate the shared "primitive" ones (i.e., plesiomorphs) from the unique "advanced" or derived ones (i.e., apomorphs) and, using only the latter ones, to redefine the genus. This discrimination between characters and stress on apomorphies forms the basis of Hennigian phylogenetic systematics. The utility of this redefined genus will be in reappraising its several presently contained species and in testing its relationships, in a phylogenetic context, with other favorine genera.

Table 1 lists the relative plesiomorphy or apomorphy, as related to all aeolids (i.e., not just members of the family containing *Godiva*), of 13 morphological characters. Polarities for constructing this table were determined by examining the character state distribution across many aeolid genera (especially those taxa generally accepted as "primitive") and by reference to outgroups such as the Arminoidea and Dendronotoidea. The majority (11) of these 13 characters exist in the apomorphic state in *Godiva* making it a relatively advanced aeolid genus. The situation remains unaltered when *Godiva* is assessed in a similar way against other genera in its family (Table 2). In this analysis, nine of the 11 characters exist in the apomorphic state. Of these nine apomorphies, however, only one is unique to *Godiva* (i.e., autapomorphic) — the curved, cuticularized, terminal penial spine. It is this character alone that must form the basis, in an exclusive sense, for the definition of the genus.

Therefore I advocate a redefinition of *Godiva* with the following exclusive set of character states: Medium-sized facelinid aeolids with smooth rhinophores; antero-lateral foot corners tentaculiform; oral tentacles moderately long; majority of cerata grouped (in two to eight rows) within arches; genital opening in front of first cluster; anus cleioproctic; uniseriate radula with protracted cusp and primary (and occasionally secondary) lateral denticles; single row of denticles on jaw's masticatory border; reproductive system with elongate ampulla, short and thick prostatic vas deferens, very elongate stalk to allosperm receptacle; penis with a curved, cuticularized, terminal spine.

This combination of characters, which is sufficient to warrant continued recognition of *Godiva* as a genus, gives *Godiva* a much narrower scope than that envisaged by Macnae (1954). By doing this, the uncertainty created by Macnae (1954) and perpetuated by Edmunds (1964), Rudman (1980) and J.C. Garcia & F.J. Garcia (1984) can be dispelled. Baba & Hamatani (1965, p. 108) have already pre-empted my action. Besides *G. quadricolor* only two other species, *G. rachelae* Rudman and Gosliner's "*G. quadricolor*" from Hawaii, now fall within the ambit of *Godiva*. Incidentally, *G. rachelae* also possesses cuticularized ridges on the apex of the jaws like those in *G. quadricolor*. Further evaluation of this new character and the longitudinal groove on the penial spine within facelinids may demonstrate them to be additional autapomorphies of *Godiva*. Indeed, an investigation of aeolids for other characters of taxonomic utility is overdue.

Eight other aeolids that have been included in *Godiva* at one time or another should now be excluded. Each is discussed separately.

*Rizzolia australis* Bergh, 1884. Macnae (1954) included this insufficiently described eastern Australian aeolid in *Godiva* when he initially diagnosed the genus. However Burn (1966, p. 31) has subsequently synonymized it with *Austraeolis ornata* (Angas), an act I wholeheartedly support. Gosliner (1980, p. 57) apparently missed this synonymy when he commented on the similarity between *R. australis* and members of the genus *Setoeolis* Baba & Hamatani. Incidentally, the genus *Rizzolia* Trinchese has now been rejected as a junior objective synonym of *Cratena* Bergh (I.C.Z.N., 1966, Opinion 776).

*Hervia ceylonica* Farran, 1905. This, plus the following three species were all placed in *Godiva* by Macnae (1954). This particular taxon is problematic because of the inadequacy of the original description. I agree with Rudman (1980, p. 164) that the species is unrecognizable.

*Cuthona* (*Hervia*) *emurai* Baba, 1937. This species has a smooth penis with a large, soft flap proximally. On penial structure alone, Baba & Hamatani (1965) proposed the new monospecific genus *Shinaneolis* to accommodate *emurai*.

*Rizzolia modesta* Bergh, 1880. Baba (1937) transferred this Japanese species to *Hervia* and, realizing the taxon then became a secondary homonym of *Hervia modesta* Bergh, 1871, amended the specific name to *japonica*. This replacement has now been sanctioned by the International Commission on Zoological Nomenclature (I.C.Z.N., 1966, Opinion 778). Macnae (1954) indicated this species belonged to *Godiva* but, because it lacks a penial spine, it should be more appropriately located in *Dondice* (as suggested by Er. Marcus, 1958, p. 66) or *Sakuraeolis* (as suggested by Baba & Hamatani, 1965).

*Hervia rosea* Bergh, 1888. This species, which has apparently not been recognized since its original

TABLE 1. Relative Plesiomorphy and Apomorphy of Aeolid Characters.

<b>Plesiomorphic</b>	<b>Apomorphic</b>
Distinct notal brim	No notal brim
Antero-lateral corners of foot rounded	Antero-lateral corners produced into tentaculiform extensions
Lamellate (or annulate) rhinophores	Rhinophores smooth or papillate, or with other ornamentation
Ceratal arrangement irregular	Cerata arranged in oblique rows or arches
Many cerata per cluster	Few cerata per cluster
Genital opening behind first ceratal cluster	Genital opening in front of first ceratal cluster
Renal pore interhepatic	Renal pore behind first post-pericardial cluster
Anus below notal brim, i.e., below ramifications of the digestive gland (pleuroproctic)	Anus more dorsal, and within interhepatic space (acleioproctic) or within (or just behind) pre-pericardial cluster (cleioproctic)
Oral glands composite	Oral glands simple
Multiseriate radula (i.e., rachidian plus lateral teeth present)	Uniseriate radula (i.e., only rachidian present)
Cusp on rachidian protracted (i.e., tooth cuspidate)	Cusp on rachidian withdrawn (i.e., tooth pectinate)
Masticatory border of jaw smooth	Masticatory border with several rows, or only a single row, of denticles
Penis simple	Penis elaborated with (soft or hard) external ornamentation and/or internal glands

TABLE 2. Relative Plesiomorphy and Apomorphy of Facelinid Characters.

<b>Plesiomorphic</b>	<b>Apomorphic</b>
Antero-lateral corners of foot produced into tentaculiform processes	Antero-lateral corners rounded
Lamellate (or annulate) rhinophores	Rhinophores smooth
Extensive branching of digestive gland in body	Reduction in branching of digestive gland in body
Many cerata per cluster	Few cerata per cluster
Cerata clustered in oblique rows	Cerata clustered in arches
One or 2 rows of cerata in each arch	More than 2 rows of cerata in each arch
Genital opening behind first ceratal cluster (i.e., interhepatic)	Genital opening in front of first ceratal cluster
Anus cleioproctic	Anus behind second ceratal cluster
Blades of rachidian with primary denticles only	Blades of rachidian with secondary denticles between primary ones or subdenticles on cusp
Masticatory border of jaw with several rows of denticles	Masticatory border with only a single row of denticles
Penis simple	Penis elaborated with (soft or hard) external ornamentation and/or internal glands

description, lacks a penial spine. Therefore it should be transferred to *Dondice* or *Sakuraeolis*, if indeed it is a member of the Facelinidae.

*Favorinus horridus* Macnae, 1954. This species is obviously not congeneric with *Eolis alba* Alder & Hancock, the type species of *Favorinus* M. E. Gray. Risso-Dominguez (1964) erected the genus *Phyllodesmiopsis* for it. Edmunds (1964) transferred it to *Godiva* on plesiomorphies of the penial and prostate glands. Rudman (1981) transferred it to *Phyllodesmium* because, amongst other characters, it had synapomorphies of flattened cerata, lack of cnidosacs and radular teeth morphology.

*Dondice banyulensis* Portmann & Sandmeier, 1960. On the basis of its anatomy, J.C. Garcia & F.J. Garcia (1984) transferred this Mediterranean species to *Godiva*. Actually it has markedly different rhinophores, radular teeth and penis to *G. quadricolor*, so it cannot be located in *Godiva*.

*Godiva rubrolineata* Edmunds, 1964. The shared similarities with *G. quadricolor* are plesiomorphs and the genital aperture opens further rearwards (i.e., below the rear limb of the pre-pericardial ceratal cluster). Neither *Sakuraeolis* nor *Shinaneolis* can accommodate this species since both are characterized by penial elaborations. Perhaps *Dondice* or *Setoeolis*, in which the penis is simple, would be more appropriate genera for this tropical western Atlantic species. Gosliner (1980, p. 57) favoured the latter genus for its placement.

## DISCUSSION OF THE FAMILY NAME

In a substantial and provocative review, Miller (1974) proposed the merging of 10 nominal aeolid families (Facelinidae, Favorinidae, Babakinidae, Pteraeolidiidae, Cratenidae, Caloriidae, Phidianidae, Myrrhinidae, Herviellidae and Glaucidae) into one because of similarities in structure of the jaws, radular teeth, glands of the alimentary system, penial glands and armature, and branching of the ducts of the reproductive system. The two autapomorphies advanced by Miller to support unification of these taxa to this single enlarged family related to possession of simple oral glands and subjective behavioural traits. I must record here that the second characteristic is not exhibited by all the species I have studied; for example, *Pteraeolidia ianthina* is neither "nervous", "fast moving", "aggressive", "voracious" nor "cannibalistic" when alive. Incidentally, the enlarged family had to take the name Glaucidae which, as Miller himself remarked, was unfortunate because *Glaucus* and *Glaucilla* are the most aberrant forms. This taxonomic necessity may have prevented some workers from embracing the entire concept (e.g., Thompson & Brown, 1984, p. 104).

In overview, it seems to me that a critical review was necessary. The earlier splitting of these aeolids between several families (most workers recognized only three or four) was excessive and it exaggerated minor differences instead of stressing fundamental similarities. This scheme therefore, completely obscured the great natural coherence of all the aeolid taxa concerned. This amalgamation has now gained general acceptance amongst opisthobranch systematists (Gosliner, 1980; Rudman, 1980, 1981; Edmunds & Just, 1983; Thompson & Brown, 1984). Edmunds & Just (1983, p. 193) have provided a diagnosis for the family. On reviewing the genera myself (from both living material and literature), I find only *Glaucus* and *Glaucilla* really do stand apart. Synapomorphies are: foot narrower than body; anterior foot corners rounded; very short oral tentacles; rhinophores on the sides of the head; cerata flattened laterally; cerata arranged on (up to 4) lateral swellings; heavily cuticularized oral tube; reduced primary denticles; pleustonic life style; inverted dorso-ventral posture. In my opinion, such a suite of autapomorphies justifies the placement of these two genera in a separate family, Glaucidae. Analogous classification schemes already exist in the Prosobranchia and Bivalvia where the Struthiolariidae and Tridacnidae, whilst obviously derived from the Strombidae and Cardiidae respectively, are given separate familial status in recognition of their radiation into new ecological zones and consequent acquisition of gross morphological novelties. That leaves the remaining nine aeolid units which, in accord with Miller (1974) I regard as monophyletic, condensed into a single family. This enlarged family must take the name Facelinidae. Whether or not the genus *Facelina* Alder & Hancock, upon which it is founded, is a synonym of *Phidiana* Gray (a most contentious and unsettled point amongst present day opisthobranch systematists) has no bearing on the eligibility of the taxon Facelinidae Vayssière, 1888 to stand as the family name. This ruling follows the (arguably unfortunate) Copenhagen

decision of the International Commission on Zoological Nomenclature that the choice of a family name should be decided by priority even when the generic name on which it is based has been abandoned as a junior synonym. That ruling is now embodied in the Principle of Priority incorporated into the present International Code [I.C.Z.N., 1985, Articles 23 (a) and (d)]. Precedents of the application of this ruling already exist in molluscan taxonomy; for example, the family name Psammobiidae Fleming, 1828 takes priority over Garidae Stoliczka, 1870, even though the genus *Psammbia* Lamarck, 1818 is a subgenus or junior synonym of *Gari* Schumacher, 1817 (I.C.Z.N. 1970, Opinion 910). Phidianidae Odhner in Franc in Grassé, 1968 is therefore a synonym of Facelinidae.

Gosliner (1980, p. 39) and Edmunds & Just (1983, pp. 193, 200) have reached the same conclusion as I do regarding the Facelinidae and Glaucidae, although they still exclude the monotypic genus *Pteraeolidia* from the Facelinidae. I also support Gosliner's (1980) additional contention that the subfamilies Facelininae, Favorininae, Crateninae and Herveiellinae are unnecessary since their contained species level taxa are probably polyphyletic.

## ZOOGEOGRAPHY

The occurrence of a population of *Godiva quadricolor* in temperate waters of southwestern Australia has thrown up another piece in a vexing zoogeographical jigsaw puzzle. This identification of *G. quadricolor*, whilst certainly providing a new record for Australia, behoves biogeographers and malacologists to account for the species' arrival because it can be explained under more than one zoogeographical hypothesis.

*Godiva quadricolor* was first described from False Bay, South Africa (Barnard, 1927). Its distribution from False Bay near the Cape of Good Hope to Port Alfred and relative abundance throughout that range, as noted by Macnae (1954), led to the assumption that it was endemic to the temperate waters of southern Africa (Edmunds, 1977). The first hypothesis for its occurrence in Western Australia does not invoke any natural mechanism, but is by way of shipping across the Indian Ocean. Either adults could have been transported on the outsides of ships' hulls [believed to have been the means responsible for the present day virtually cosmopolitan distribution of at least one other nudibranch, *Thecacera pennigera* (Willan, 1976; Willan and Coleman, 1984)] or larvae could have been transported within the ballast tanks of seagoing vessels (Carlton, 1985; Williams & Griffiths, 1986). Entrained ballast water is a much underestimated present day mode of transoceanic dispersal of marine organisms. This shipping hypothesis would appear to have more evidence to support it than any alternative hypothesis. By this, I refer firstly to the recent colonization of several other foreign marine organisms in the same area of southwestern Australia, essentially that centered on the port of Fremantle. Documented cases amongst the Mollusca are those of the bivalves *Theora lubrica* (Chalmer et al., 1976) and *Musculista senhousia* (Slack-Smith & Brearley, 1987). Second is the apparent confinement, at present, of *G. quadricolor* to the Fremantle-Cockburn Sound area. Third is the fact that Western Australia receives approximately half the total Australian national commercial shipping each year (Williams et al., 1982). Finally is the undisputed introduction by shipping of another endemic temperate southern African nudibranch, *Polycera capensis*, to Sydney Harbour in the 1920's (Burn, 1978). Edmunds (1977) put forward a protocol in order to recognize marine animals that might have crossed, or be capable of crossing, oceans on boat hulls. At all stages of the organism's life cycle it should be possible to show that: (1) suitable foods do grow on boat hulls; (2) some individuals are occasionally found on boats; (3) the species is restricted on one side of the ocean to the vicinity of ports (at least to begin with); (4) the species is morphologically identical on both sides of the ocean. With the knowledge that Edmunds (1977) did actually find one specimen of *G. quadricolor* on a boat hull in Ghana, the last three criteria are all satisfied unequivocally in the case of *G. quadricolor*.

It is possible that some of the other endemic South African molluscs that have turned up in southwestern Australia such as *Haliotis spadica* (Macpherson, 1953 as *Haliotis sanguinea*), *Nassarius kraussianus*, *Bullia annulata* and *Cabestana cutacea dolaria* (Wells & Kilburn, 1986) might also have been introduced by shipping. Yet none of these species has established a breeding population, as judged by persistence of records through time. Alternatively some as yet unexplained natural

zoogeographic mechanism could have allowed them, and *Godiva quadricolor* too, to cross the Indian Ocean from west to east.

Gosliner's (1980) report of *Godiva quadricolor* from Hawaii, if correct, would have allowed another zoogeographical hypothesis account for the presence of *G. quadricolor* in southwestern Australia; that of possession of a continuous Indo-Pacific distribution. However, I feel significant objections have eliminated this hypothesis. First is Dr Gosliner's own present belief (pers. comm., 1986, 1987) that Hawaiian and South African specimens are not conspecific. Since his examination of Hawaiian animals, Dr Gosliner has studied South African ones at first hand and he now recognizes significant morphological differences do exist (see Remarks section). Second is Edmunds' (1977) query that, if *G. quadricolor* were to have a continuous Indo-Pacific distribution, it should have been found at other intervening localities in the Pacific Ocean where nudibranch faunas have been relatively well investigated such as Japan, the Marianas Islands, the Marshall Islands, New Caledonia, eastern Australia and New Zealand. This is particularly true since *G. quadricolor* is essentially an intertidal species, and also it is relatively large and distinctively [Edmunds (1977, p. 303) said "gaudily"] coloured.

In closing, I suggest time itself will be the best test between the competing hypotheses of man-aided transportation or natural transoceanic dispersal. If the Western Australian population persists and expands its range and/or if *Godiva quadricolor* occurs in other temperate ports in the world, the former hypothesis will be vindicated.

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